



Hedgerows interact with forests to shape the abundance of mesopredators and their predation rate on eggs in farmland landscapes

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ARTICLE INFO

Editor: Damià Barceló

Keywords:

Artificial nest

Corvids

Land use

Landscape structure

Road density

Predator management

ABSTRACT

Nest predation is the main cause of reproductive failure, particularly in ground-nesting birds on farmlands. Understanding the links between nest predation and habitat change can help design effective management schemes to constrain the negative impact of predation pressure on birds. However, the mechanisms underlying the relationships between landscape attributes, predator distribution, and nest predation are still unclear. Here, we use an experimental approach to examine the effects of distance to the hedgerow as well as hedgerow and forest densities on the abundance of major mesopredators of ground nests of our study area (i.e., corvids) and on the predation rate of artificial ground nests ($n = 2576$). We found evidence that landscape configuration influenced predation patterns differently depending on the predator species. Nest predation by corvids was more likely in homogeneous and open agricultural landscapes with a low density of forest and hedgerows, whereas predation by other predators was more likely close to hedgerows. Nest predation by corvids and the abundance of corvids also tended to be lower in landscapes dominated by grasslands. Other variables such as road density and distance to human settlements had contrasted effects on the likelihood of a nest being depredated by corvids, i.e., no effect with proximity to human settlements and decreasing trend with road density. Altogether, our results suggest that landscape features interact with mesopredator distribution and their predation rates of ground nests. Therefore, from a conservation and management perspective, a heterogeneous agricultural landscape that includes a mixture of crops associated with patches of forests, hedgerows, and grasslands offering alternative food to generalist predators should contribute to reducing ground-nesting bird predation.

1. Introduction

Farmlands are complex mosaics of extensive crops mixed with semi-natural elements (Fahrig et al., 2011; Martin et al., 2019; Sirami et al., 2019), that are used to sustain high levels of biodiversity. However, over the second half of the twentieth century, such landscapes have profoundly changed through agricultural intensification (García-Martín et al., 2021), which led to considerable shifts in landscape structure, e.g., hedgerow network impoverishment and landscape homogenisation (Benton et al., 2003; Gámez-Virués et al., 2015). Land management intensification has also affected biodiversity and ecological processes (Allan et al., 2015; Emmerson et al., 2016; Newbold et al., 2015), including food webs and predator-prey relationships (Manton et al.,

2019; Rusch et al., 2016; Shapira et al., 2008).

Agricultural intensification, together with top predator extirpation and game releases for hunting purposes (Pringle et al., 2019), have contributed to triggering changes in the abundance of generalist mesopredators (Roos et al., 2018; Terraube and Bretagnolle, 2018) and prey species dynamics (Andrén, 1992; Andrén, 1995; Bayne and Hobson, 1997), though other factors are also involved in predation rates (Kentie et al., 2015; Madden et al., 2015). Since top predators have not recovered enough in most areas (Terraube and Bretagnolle, 2018), alternative methods have been established to mitigate the impacts of mesopredators, such as lethal predator controls (trapping, shooting) or predator exclusion. However, the effectiveness of lethal predator control in affecting predator demographic parameters and enhancing prey

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<https://doi.org/10.1016/j.scitotenv.2023.165712>

Received 22 March 2023; Received in revised form 19 July 2023; Accepted 20 July 2023

Available online 28 July 2023

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species conservation has been questioned (Dinkins et al., 2016; McMahon et al., 2020; Smith et al., 2010). Predator exclusion provides interesting results at a local scale (Malpas et al., 2013; Melstrom and Horan, 2013), but remains difficult to apply at a broader scale (Rickenbach et al., 2011). Landscape management has been suggested as a promising avenue and has indeed shown positive effects (Dunn et al., 2016; Laidlaw et al., 2017), either by lowering the predation success rate or by improving habitat quality by providing alternative food resources (natural grasslands, hedges) for predators (Wilson et al., 2005).

In farmlands, studies have reported that predation shapes both nesting success and chick survival, however, the effects of landscape attributes on predation patterns are still unclear (Kauffman et al., 2007; Tewksbury et al., 2006), as is the interplay between habitat structure, predation risk, and predator distribution (Chiavacci et al., 2018; Tewksbury et al., 2006; Van Der Vliet et al., 2008). Forest density (Andrén, 1992; Small and Hunter, 1988), edges or hedgerows (Batáry and Báldi, 2004; Hinsley and Bellamy, 2000), and anthropogenic attributes (e.g., roads) (Pescador and Peris, 2007; Silva et al., 2019) affect nest predation dynamics both at a local and broader scale (Ellis et al., 2020). However, habitat structure, predation risk, and predator community and distribution are interconnected, making ecological mechanisms underlying predation dynamics hard to decipher, particularly in the network of mesopredators and ground-nesting birds (Lahti, 2009). Several landscape attributes might influence prey-predator interactions. Firstly, hedgerows can act as corridors, particularly for mammalian predators (Graham et al., 2018; Pelletier-Guittier et al., 2020) and provide advantageous perching/lookout positions for avian predators like corvids, presumably enhancing predation rates close to edges. Furthermore, hedgerows might be attractive to predators because of their high prey density and concealment, hence it also might increase predation rates close to hedgerows. However, how hedgerows interact with other landscape attributes, such as forest density and crops is unclear. Secondly, forests and land use cover might also determine the availability of prey for generalist predators. Considering the landscape structure context, predictions of hedgerow effects might be less straightforward when, for instance, the availability of food resources is similar in hedgerows to some land uses. Thirdly, in open farmlands with rare forest patches, forest patches might lead to a spill-over of generalist predators into the adjacent farmland matrix, hence increasing nest predation in such mixed landscapes (Andrén, 1995). Fourthly, anthropogenic features might also shape predation patterns through their effect on mesopredator abundance. For instance, roads and human-supplied food resources may attract opportunistic vertebrate species that actively search for carrion along roads or generalist species adapted to living with humans. Finally, nest predator communities differ in response to landscape attributes (Andrén, 1992; Chalfoun et al., 2002). Although the social status of predators is important for assessing the impact of avian predators on nest predation dynamics (Bravo et al., 2020), whether nest predators respond to landscape attributes differently depending on social status has received little attention.

In this study, we designed an experimental set-up with artificial ground nests ($n = 2576$) in an intensive agricultural landscape. Previous results in our study area have shown that corvids were the main predators of ground nests (Bravo et al., 2020). To quantify the predation rate on ground nests, accounting for both the abundance of mesopredators and landscape features, we first investigated how the distance to hedgerow, hedgerow density, and forest density affected the probability of a nest being depredated. While land uses and anthropogenic features are expected to affect predation patterns (i.e., by improving or limiting the availability of food resources for predators), we mainly hypothesised that the hedgerow effect on predation rate would differ depending on the habitat use and density of potential predators (Andrén, 1995). Proximity to hedgerows is expected to affect avian predators, such as corvids, differently to other predators such as mammals. Since predation patterns should be affected by the availability of forest patches or landscape connectivity (e.g., density of hedgerow network), we

hypothesised that the predation rate would decrease as the density of hedgerows and forests increases (Andrén, 1992). Then we assessed how the abundance of mesopredators changed with the same landscape attributes (hedgerow and forest density). Since reproductive status (breeder or not) and land use (i.e., as a proxy of food resources) may affect the distribution of predators, we hypothesised that the abundance of nest predators (e.g., corvids) would increase in homogeneous landscapes with low hedgerow and forest density (Andrén, 1995). Finally, if landscape shapes the distribution of predators and thus their predation rates on ground nests, the relationship between landscape variables (mainly hedgerows and forest) and the probability of a nest being depredated is expected to show a pattern similar to the one between landscape variables and the abundance of mesopredators. Prey-predator systems are complex, and as is the case in many ecological systems (Díaz and Concepción, 2016; Fernández et al., 2002), non-linear relationships between predictors and response variables are expected. For this reason, we have considered quadratic effects to capture potential non-linear relationships between landscape predictors and egg predation and corvid abundance.

2. Methods

2.1. Study area

The study was carried out in the LTSER ‘Zone Atelier Plaine & Val de Sèvre’, central Western France (46°15 N, 0°30 W, [Fig. 1](#)), which comprises 450 km² of intensive agriculture, mostly dedicated to cereal production (see [Bretagnolle et al. \(2018\)](#) for a general description of the site). The area is characterised by an open farmland landscape, almost flat (altitude 40 to 100 m asl) with a network of hedgerows (that is, ‘bocage’) and small forest patches ([Fig. 1](#)). The hedgerows are generally 2 to 5 m high and 1 to 10 m wide, with hawthorns (*Crataegus monogyna*), blackthorns (*Prunus spinosa*), and common blackberries (*Rubus fruticosus*) as the main components. The most common crops are wheat (33.8 %), meadows (13.5 %), corn (9.6 %), sunflower (10.4 %), oilseed rape (8.3 %), and pea (2 %). The community of mesopredators includes raptors like harriers (*Circus pygargus*, *C. cyaneus*, and *C. aeruginosus*), corvids like carrion crows (*Corvus corone*), Eurasian magpies (*Pica pica*), western jackdaws (*C. monedula*), rooks (*C. frugilegus*) and Eurasian jays (*Garrulus glandarius*), and small carnivores like red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), weasels (*Mustela nivalis*) and domestic cats (*Felix catus*) ([Bravo et al., 2022](#)). The study area is an important breeding site for protected bird species and game bird species. The presence of many species covered by the EU Birds Directive led to the designation of a NATURA 2000 site in 2004 (FR5412007) on c. half of the LTSER.

2.2. Predation experiment

We monitored 2576 artificial nests set up at 112 sampling points during three breeding seasons, 2017–2019. The experimental design has been fully detailed in [Bravo et al. \(2022\)](#). A sampling point consisted of a given location, at which several nests were placed at 30 m intervals along transects ([Fig. 1B](#)). The sampling points were selected with a stratified scheme, according to the hedgerow density and the forest fragments, in order to span a maximum range of each of these elements across sampling points, while maintaining as low as possible paired correlations between these elements. In 2017 and 2018, two transects per sampling point were set in two adjacent fields while, in 2019, only one transect was set. Although the number of transects per sampling site differed in the different years, we did not detect any spatial autocorrelation. The average distance (\pm SD) between transects in 2017 and 2018 was 129.4 ± 52.91 m (range 52.16–355.71 m). Transects were set parallel to the hedgerow, randomly at one of either four distances from the hedgerow (one distance per sampling point): 10 m, 30 m, 50 m, and 70 m.

Nests consisted of eggs fabricated from off-white nontoxic odourless

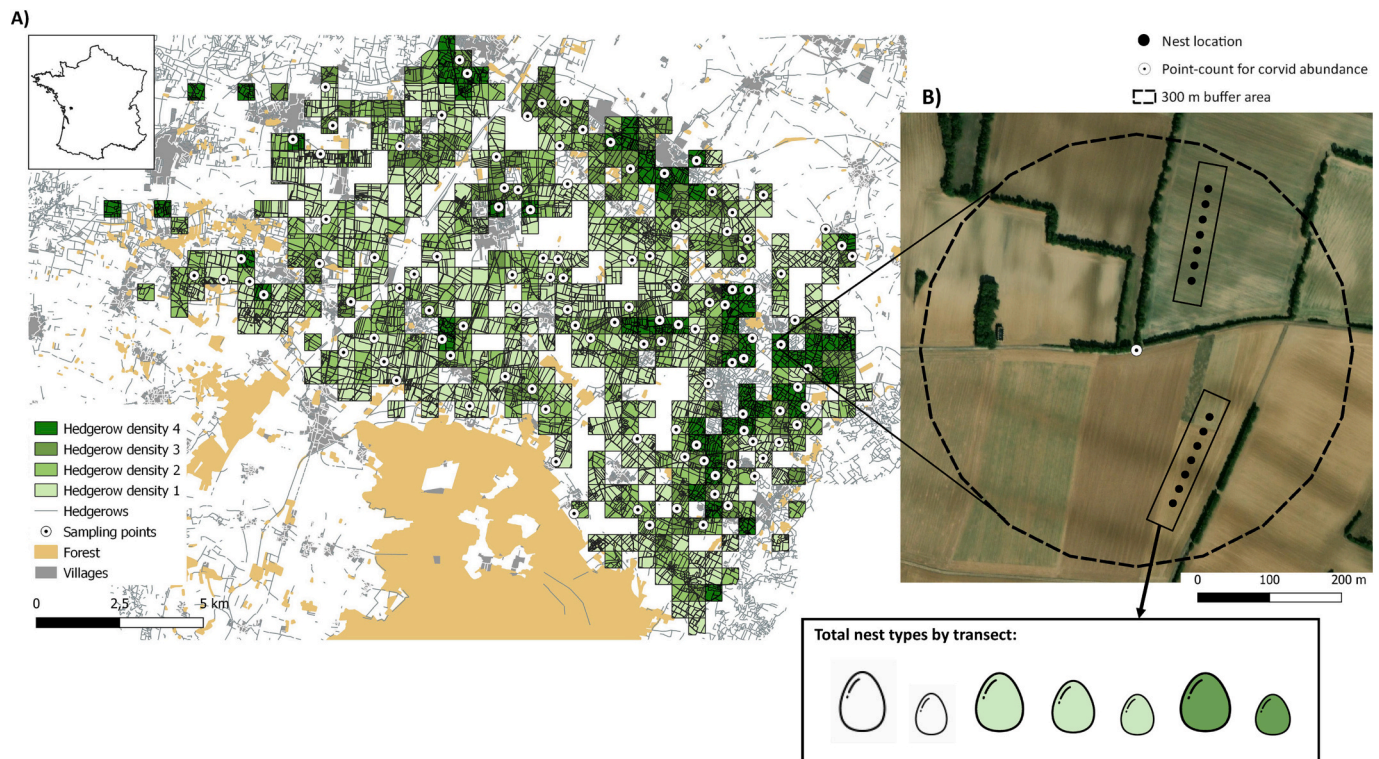


Fig. 1. A) Location of the sampling points in the study area within the Long-Term Social-Ecological Research (LTSER) site ‘Zone Atelier Plaine & Val de Sèvre’ (France). Note the sampling points were stratified according to hedgerow density. B) Image of a sampling point showing the location of the artificial nests ($n = 2576$) and the location of the point count to estimate the corvid abundance. Note that transects were set parallel to the hedgerow at 10 m, 30 m, 50 m, and 70 m (one distance per sampling point).

plasticine (J. Herbin plastiline, Chelles, France). Each nest was formed as a shallow depression in the soil and contained two identical plasticine eggs fixed by a thin wire and a nail in the ground to prevent predators from carrying them away. Nest location was recorded by GPS position, no markers were placed.

Nests were set up weekly from 26th March to 19th June each year, allowing detailed analysis of seasonal effects. Nest location was moved by at least 100 m from the location used in previous years to avoid a memory effect. Nests were exposed to predators for 7 consecutive days in 2017 and 15 days in 2018 and 2019. This time allows to mimic the egg-laying period (when individuals leave their nests open and are not incubating the eggs), which varies from 2 to 7 days for little bustard or Montagu’s harrier and is up to 15 days for partridges, three ground nesting birds typical of our landscapes. As (i) the time of nest exposition varied among years and daily survival rates (DSR) were not constant with time showing a quadratic pattern throughout the experiment (Appendix 1) and (ii) our previous study showed that the nest halftime was 3 days on average (Bravo et al., 2022), we used nest predation recorded on day 3 as a standardised measure of predation rate to control for the time effect on the predation rate.

We deployed several egg types per sampling point to simulate predation rates by different predators (Fig. 1B). We used three categories of egg sizes: large (5×3 cm), medium (3.5×2.5 cm), and small (2.5×1.5 cm) and three colours (white-off, light green, and dark green). In 2017, four nest types were deployed per sampling point: large white, small white, large light green, and small light green. In 2018 and 2019, five nest types were deployed per sampling point: large white, small white, large dark green, small dark green, and medium light green (see Appendix 2).

We considered nests to be depredated when one of the eggs had been damaged. Predator species were identified by tooth and bill imprints in plasticine eggs (see Bravo et al. (2020)). Predator species were identified as corvids or other species, such as mammals, small mammals, and

raptors. Nests destroyed by farming practices ($n = 21$) were removed from the analyses.

2.3. Estimating corvid abundance

Corvid abundance (carrion crow and magpie) was estimated during the breeding season of the three years (2017–2019) at each sampling point ($n = 112$). We tried to set point counts as close as possible to nests, with mean (\pm SD) distances between point count and artificial nest location being 145.4 ± 120.7 m. Corvids were counted using 10-min duration point counts repeated four times per breeding season, at about 2-week intervals, spread from 29th March to 19th June each year. In each visit, all auditory and visual contacts, their accurate location, and the behaviour of every single corvid individual were recorded within a 300-m radius (i.e., 28.3 ha) around the observer. The minimum territory size of a magpie is 2.53 ha (Baeyens, 1981) and 9 ha for a carrion crow (Yom-Tov, 1974). Surveys were carried out within 4 h of sunrise while avoiding rainy or strong wind conditions (Luginbuhl et al., 2001). We repeated counts to discriminate territorial breeders from non-breeders in each sampling point. The presence of territorial breeders was determined using a combination of proxies. Firstly, the nests (whether active or inactive) were located in early spring (before the bud burst, typically a early March). Secondly, corvid behaviour was used as a proxy to indicate breeding and territorial behaviour, such as bringing nest material, feeding, and territorial defense against other corvids, alarm calls, and attacking raptors (Röell and Bossema, 1982; Tapper et al., 1996). And thirdly, by analysing the four samples per point: if a pair was observed at least in 2 out of 4 counts, it was assumed to be a territorial pair. The absence of a territorial pair/breeder was concluded otherwise, i.e., if no nest had been observed, no breeding or territorial behaviour had been observed in any of the four samples, and no pair was seen twice. Then, the total number of pairs per sampling point was obtained, and the abundance of non-breeders (floaters) was determined as the

maximum number of corvids recorded on a given point minus the number of breeders.

2.4. Landscape variables

Around each artificial nest and point count, we assessed the following landscape variables: i) hedgerow density, forest density, and distance to the closest hedgerow as proxies of landscape structure, ii) the proportion of different land uses (i.e., cereals, grasslands, spring crops, oilseed rape and others, see below) as a proxy of alternative food for mesopredators, for instance, cereal crops harbour fewer insects than others land uses (Díaz and Tellería, 1994), and iii) anthropogenic variables such as distance to human settlements and road density (see Table 1 for details). Landscape variables were quantified, from LTSER land cover monitoring (see Bretagnolle et al. (2018)) and the database of the Institut National de l'Information Géographique et Forestière (BD TOPO®). We used QGIS (version 3.4.12). We selected a 300 m buffer from each artificial nest and from each point count to calculate the landscape variables since other buffer sizes (i.e., 100, 200, 400, and 500 m) led to lower statistical support in the models investigating corvid predation or corvid abundance (see Appendix 3).

Given that hedgerow density might depend on the width of the hedgerow and hedgerow width is quite variable in our study area, hedgerow density was defined as the surface (m^2/ha) of tree lines forming a contiguous network across the farmed landscapes within the 300 m buffers. Polygons (and thus hedgerow surfaces) were created from the tree lines and width of hedgerows, which varied from 5 m to 20 m wide. The forest density was defined as the surface of forest (m^2/ha) patched within the 300 m buffers.

Within the 300 m buffers, we extracted five types of land use according to the type and structure of vegetation: cereals (mainly wheat), grasslands (meadows), spring crops (sunflowers and corns), oilseed rape and other crops (such as ryegrass, wax, peas, and lens). As proportions of land uses were correlated, we ran a Principal Component Analysis (PCA) to extract two uncorrelated synthetic variables. PCA was conducted separately for predation and corvid abundance, and we extracted the first two principal components as they accounted for 58.7 % and 56.3 % of the total variances, respectively (see Appendix 4 for details). Loadings related to land uses indicated that i) when PC1 increased, the proportions of cereal crops increased in the landscape whereas spring crops and grasslands decreased and ii) when PC2 increased, the proportions of spring crops increased whereas grasslands decreased (Appendix 4).

Table 1

Landscape variables used to predict the probability of nest predation and corvid abundance in western France. For predation models, landscape variables were calculated around the location of each artificial nest, whereas, for models of corvid abundance, they were calculated around the point count location (see methods).

Independent variable (unit)	Description	Predation model			Corvid abundance model		
		Mean	SD	Range	Mean	SD	Range
<i>Landscape structure</i>							
Distance to hedgerow (m)	Distance from the artificial nest to the nearest hedgerow	42.56	21.15	[6.64–81.77]	–	–	–
Hedgerow density (m ² /ha)	Surface of tree lines forming a contiguous network across the farmed landscapes in a 300 m buffer	546.64	318.07	[42.69–1573.1]	536.44	289.1	[62.46–1265.64]
Forest density (m ² /ha)	Surface of forest patches in a 300 m buffer	78.44	130.70	[0–653.97]	63.15	81.22	[0–566.33]
<i>Alternative food variables</i>							
Cereal cover (%)	Proportion of area within 300 m buffer with cereal crops such as wheat and barley	36.06	20.14	[0–82.85]	38.87	21.20	[0–95.91]
Grassland cover (%)	Proportion of area within 300 m buffer with grassland crops such as meadows and alfalfa	19.86	17.60	[0–81.79]	17.26	17.31	[0–87.09]
Spring crop cover (%)	Proportion of area within 300 m buffer with spring crops such as sunflower and corn	24.73	18.96	[0–89.15]	24.38	19.32	[0–92.99]
Oilseed rape crop cover (%)	Proportion of area within 300 m buffer with oilseed rape crops	4.48	8.11	[0–31]	3.57	7.83	[0–51.64]
Other crops cover (%)	Proportion of area within 300 m buffer with other crops such as ryegrass, wax, peas, and lens	8.39	10.85	[0–51.36]	8.84	11.88	[0–87.09]
<i>Anthropogenic variables</i>							
Distance to human settlements (m)	Distance to the nearest human settlement such as a house, farm, or village	306.72	197.35	[14.6–1309.3]	287.51	195.29	[17.95–1193.55]
Road density (m/ha)	Total length of paved roads in a 300 m buffer	47.38	14.36	[11.8–97.1]	46.18	14.53	[21.55–94.21]

Two variables were assessed as proxies of human disturbances: the distance (m) between the experimental nest or the point count location and the nearest human settlement (i.e., houses, industrial and agricultural buildings); and road density as the total length (m/ha) of paved roads (motorway, national, departmental and communal roads) within the 300 m buffer.

We also accounted for how a specific crop type in the immediate vicinity of the nest influenced the predation rate (hereafter, crop type; Bravo et al., 2022). For this, crop types were regrouped according to vegetation type and structure as follows: cereals (mainly wheat and barley), grasslands (meadows and alfalfa), spring crops (sown in late February and after, including mainly sunflower and corn), and other crops (oilseed rape, ryegrass, wax, peas, and lens).

2.5. Statistical analysis

2.5.1. Predation rates

First, we investigated the relationship between landscape structure and the probability of a nest being depredated (i.e., on day 3) using generalised linear mixed-effects models (GLMM) with a binomial error distribution (logit link function) including distance to hedgerow, hedgerow density, and forest density (all standardised), and all two-way interactions as predictors. As predictors might affect the probability of predation in a non-linear way, we included their quadratic term. We also included the two axes of the PCA that describe the proportion of land uses surrounding the experimental nest location and their two-way interactions with the predictors of landscape structure cited above. As crop type in which the nests were located may also affect the predation probability (Bravo et al., 2022), crop type (with four levels, cereal, grassland, spring crop, and others) and its two-way interactions with distance to hedgerow were included as predictors. To account for a possible temporal effect in our models, year and julian day were also included. In a last step, to investigate whether anthropogenic variables affected the relationship between landscape structure and probability of nest predation, we run a model including road density and distance to human settlements and their two-way interactions with the predictors of landscape structure (i.e., hedgerow density, forest density and distance to hedgerow). We run separate models with predation carried out by corvids (i.e., the main mesopredators of depredating nests) and other predators (i.e., mammals and raptors).

Potential confounding factors were present in our experimental design. First, since we showed that egg types affected the probability of a

nest being depredated in a previous study (Bravo et al., 2022), this variable was also included as a random factor (with seven levels, large white, small white, large dark green, small dark green, large light green, medium light green, and small light green). And second, to account for the spatial structure of our data set, we included the transect id, nested in the sampling point, as a random factor. Moran's I correlograms from the residuals of models using 'pgirmess' package showed the lack of spatial autocorrelation between experimental nests (Appendix 6).

2.5.2. Abundance of corvids

We analysed the effects of the same landscape parameters on corvid abundance, with similar procedures and structured models. The first model included standardised landscape structure variables (hedgerow density, forest density, their quadratic terms, and the two-way interaction as predictors) using a generalised linear model (GLM) with Poisson error distribution (logit link function). Land use proportion around the sampling point was then included with the first two PCA axes (Appendix 4) and the two-way interactions between PCA and landscape structure. Then anthropogenic variables (road density and distance to human settlements) were added. We run models on the abundance of corvid breeders and floaters separately.

Corvid abundance varied significantly between years, both in breeders ($\chi^2 = 32.60$, $df = 2$, $p < 0.01$) and floaters ($\chi^2 = 33.04$, $df = 2$, $p < 0.01$; see Appendix 5 for details). As the effect of year on corvid abundance was not the focus of this article, we summed the sightings of individuals observed over the three years. In this way, we gave greater weight to sampling points where corvids were observed during the 3 years in the same area. We checked for the lack of spatial autocorrelation in the model residuals using Moran's I correlograms (Appendix 6).

2.5.3. Relationship between corvid predation and corvid abundance

To investigate the relationship between corvid predation and corvid abundance, we run the first model of corvid predation which included landscape variables as predictors (i.e., distance to hedgerow, hedgerow density, forest density, their quadratic terms, and the two-way interaction, PCA axes and crop type). This model was then compared with a model now including, in addition to previous variables, corvid breeder abundance and another one including corvid floater abundance. If landscape effects on nest predation were due to landscape effect on predator abundance, we predict that the effect size (i.e., Odds ratio) of these landscape effects would lose significance when corvid abundance is included in the models (Díaz et al., 2013).

For all models, we used 95 % confidence intervals (CI) to investigate

the significance of factors on the probabilities of a nest being depredated and corvid abundance. We considered that there was not a consistent effect when 95 % CI overlapped the zero value. We used the package 'lme4' to run GLMM (Bates et al., 2015). The coefficients of the graphs were extracted from the minimal model including only significant predictors. All models were tested using R version 4.0.3 (R Core Team, 2021).

3. Results

From the experimental nests ($n = 2576$), 16.28 % were depredated ($n = 416$) during the 3-day period with 84.4 % of nests depredated by corvids and 14.9 % by other predators (mammals and raptors).

3.1. Effects of landscape features on predation rates

The effect of distance to the hedgerow on the probability of a nest being depredated by corvids varied significantly with the crop type. Corvid predation decreased with distance to hedgerows in nests located in spring crops. In contrast, no significant effect of distance effect was observed for nests located in cereal crops (Fig. 2A). Hedgerow and forest density also affected the corvid predation rate in a complex quadratic manner (Table 2). The corvid predation rate was minimal (3–5 %) at medium-high hedgerow density (i.e., 600–1200 m²/ha) with forests being either absent or highly present (Fig. 3). The probability of predation by other predators was highest when closest to the hedgerow regardless the crop type (Fig. 2B, Table 2), while neither the hedgerow nor the forest density affected this probability (Table 2B). Crop type did not affect predation probability by other predators. Furthermore, the probability of corvid predation decreased by 45 % during breeding season (i.e., julian day), whereas predation by others tended to increase slightly with julian day (Table 2, Appendix 5: Fig. S6). Therefore, predator type (i.e., corvids vs. non-corvids) was crucial in understanding the effects of landscape structure on the predation rate of ground nests.

Corvid predation rate decreased as the proportion of cereal crops (i.e., PC1) increased from 0 to 0.8 in the landscape (Fig. 4). However, this effect depended on the crop type. Specifically, it decreased by 50 % when the nest was located in spring crops, but remained unchanged in nests located in cereal crops. Corvid predation rate was not influenced by the proportion of grasslands (i.e., PC2) (Table 2). Conversely, the nest predation by other predators was not affected by either of the two PCA axes (Table 2). Finally, the probability of corvid predation tended to decreased by 30 % with an increase in road density from 20 to 60 m/ha

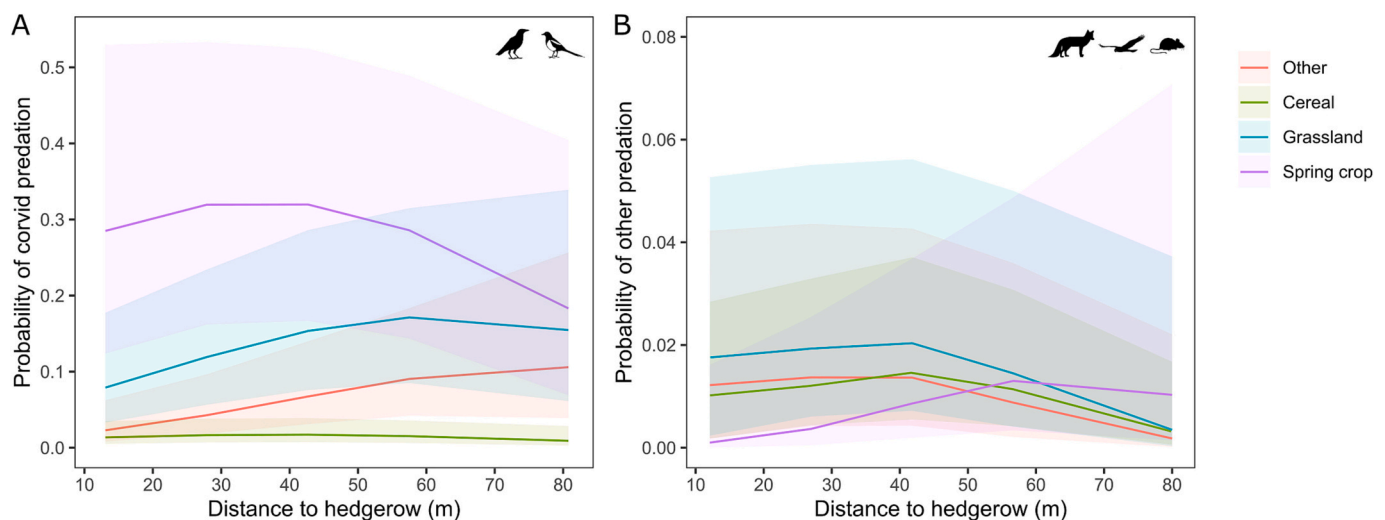


Fig. 2. Quadratic effect of the distance to hedgerow on the probability of a nest being depredated by corvids (A) and other predators (B) splitting by the crop type in which nest is located (spring crops, grasslands, cereal crops, and others). Full line is the predicted values (with ± 95 % CI) extracted from GLMM detailed in Table 2.

Table 2

Effects of the distance to hedgerow, hedgerow density, forest density, and their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the probability of a nest being depredated by corvid (left) or other predators (right) using GLMM (binomial, link = logit). PC1 and PC2 are the first two axes of PCA in land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5). The reference level for year is 2017 and *Others* for crop type (i.e., crop type in which nest was located). Asterisks indicated significant factors (i.e., 95 % CI no overlapped the zero value).

Explanatory variables	Corvid predation model				Other predation model			
	Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI
(Intercept)	-1.19	0.75	-2.66	0.28	-6.03	1.17	-8.32	-3.75
Distance to hedgerow	0.65	0.21	0.25	1.06*	-0.22	0.50	-1.20	0.75
Distance to hedgerow ²	-0.12	0.10	-0.31	0.08	-0.57	0.22	-1.01	-0.13*
Hedgerow density	-0.32	0.15	-0.61	-0.02*	0.06	0.24	-0.40	0.53
Hedgerow density ²	0.22	0.13	-0.04	0.47	-0.16	0.23	-0.61	0.30
Forest density	-0.10	0.31	-0.70	0.50	-0.65	0.50	-1.62	0.32
Forest density ²	-0.21	0.23	-0.67	0.24	-0.08	0.41	-0.88	0.72
PC1	-0.45	0.19	-0.82	-0.09*	-0.21	0.39	-0.97	0.55
PC2	-0.02	0.16	-0.32	0.29	0.31	0.32	-0.31	0.93
Crop type (Cereals)	-1.34	0.27	-1.87	-0.82*	0.04	0.46	-0.87	0.95
Crop type (Grasslands)	0.97	0.27	0.44	1.49*	0.63	0.56	-0.46	1.72
Crop type (Spring crops)	1.79	0.36	1.09	2.49*	-0.46	0.80	-2.03	1.11
Julian day	-0.01	0.00	-0.02	0.00*	0.01	0.01	-0.01	0.02
Year (2018)	-0.59	0.22	-1.01	-0.16*	1.14	0.43	0.29	1.98*
Year (2019)	-0.12	0.27	-0.64	0.40	1.67	0.48	0.73	2.60*
Distance to hedgerow × Crop type (Cereals)	-0.73	0.27	-1.26	-0.20*	0.28	0.54	-0.78	1.34
Distance to hedgerow × Crop type (Grasslands)	-0.29	0.26	-0.79	0.22	0.19	0.65	-1.08	1.47
Distance to hedgerow × Crop type (Spring crops)	-0.75	0.28	-1.31	-0.20*	1.30	0.78	-0.22	2.83
PC1 × Crop type (Cereals)	0.72	0.24	0.26	1.19*	-0.04	0.41	-0.84	0.76
PC1 × Crop type (Grasslands)	0.40	0.23	-0.05	0.85	0.39	0.47	-0.53	1.32
PC1 × Crop type (Spring crops)	0.30	0.26	-0.22	0.82	0.14	0.58	-0.99	1.27
PC2 × Crop type (Cereals)	0.15	0.23	-0.30	0.60	-0.16	0.37	-0.89	0.57
PC2 × Crop type (Grasslands)	-0.05	0.20	-0.45	0.35	-0.01	0.47	-0.92	0.90
PC2 × Crop type (Spring crops)	0.32	0.23	-0.13	0.76	-0.18	0.52	-1.20	0.84
Hedgerow density × Forest density	-0.09	0.22	-0.51	0.33	0.88	0.41	0.08	1.68*
Distance to hedgerow × Hedgerow density	0.19	0.11	-0.01	0.40	-0.46	0.27	-1.00	0.07
Distance to hedgerow × Forest density	-0.04	0.16	-0.35	0.27	0.93	0.39	0.17	1.68*
PC1 × Hedgerow density	0.12	0.11	-0.10	0.33	-0.29	0.19	-0.67	0.09
PC1 × Forest density	0.13	0.16	-0.19	0.45	-0.30	0.30	-0.89	0.29
PC1 × Distance to hedgerow	0.15	0.09	-0.03	0.34	0.12	0.19	-0.25	0.49
PC2 × Hedgerow density	0.09	0.09	-0.09	0.27	0.16	0.19	-0.21	0.52
PC2 × Forest density	-0.09	0.16	-0.40	0.22	-0.08	0.29	-0.64	0.48
PC2 × Distance to hedgerow	0.04	0.09	-0.13	0.21	0.10	0.19	-0.27	0.47

(Estimate ± SE = -0.39 ± 0.24; 95 % CI = -0.90 — 0.08) but it did not change with distance to human settlements (-0.23 ± 0.26; 95 % CI = -0.74 — 0.29). Road density and distance to human settlements did not affect nest predation by other predators (-0.45 ± 0.46; 95 % CI = -1.36 — 0.45; 0.10 ± 0.18; 95 % CI = -0.24 — 0.45, respectively).

3.2. Effects of landscape features on corvid abundance

The mean number of territorial corvid breeders was 2.41 individuals (± 0.84, range 0–6). They were observed in 42.0–76.8 % (depending on the year) of the sampling points (Appendix 5). The mean number of corvid floaters was 3.81 individuals (± 6.77 individuals, range 0–58). They were observed at 67.9–81.3 % of the sampling points. Considering the sum of corvid individuals over the three years, the mean of territorial corvid breeders was 4.7 individuals (± 2.23, range 0–10) and of floaters was 8.34 individuals (± 10.62, range 0–62). Territorial corvid breeders and corvid floaters were present in 89.3 % and 99.1 % of sampling, respectively (Appendix 2).

The abundance of corvid breeders and floaters varied significantly with forest and hedgerow densities in a complex way as effects were quadratic and sometimes interacting (Table 3). The clearest signal was observed in corvid floaters with more individuals in poor hedgerow/forested landscapes (Fig. 5B). The abundance of floaters was mainly affected by hedgerow density, with a strong decrease from 25 to 10 individuals on average when hedgerow density increased from 200 to 1200 m²/ha (Fig. 5B). In contrast, the abundance of corvid breeders showed a quadratic relationship with forest density (Table 3A), similarly to the probability of corvid predation. The number of breeders was low

(i.e., 2 individuals or 1 pair) at high forest density (i.e., 500 m²/ha), and increased to reach 4 individuals (or 2 pairs) when there were no forest patches in the landscape and at 600 m²/ha of hedgerow density. The abundance of breeders was very similar to the probability of corvid predation being maximal (i.e., 6 individuals or 3 pairs) when the forest density was around 300 m²/ha and there were no or many edges (Fig. 5A).

The abundance of corvid breeders was not affected by the proportion of land uses, conversely to corvid floater abundance, which responded strongly and negatively to the proportion of cereal crops (i.e., PC1), and positively to the proportion of spring crops (i.e., PC2; Table 3B, Appendix 7: Fig. S9). The two interactions PC1 × hedgerow density and PC2 × forest density significantly affected corvid floater abundance (Table 3B). The abundance of corvid floaters decreased with hedgerow density when there were no cereals in the area, while the effect of hedgerow density vanished when the landscape was dominated by cereals (Appendix 7: Fig. S10). A similar pattern was found with forest density and spring crops (Fig. S10).

The road density and the distance to human settlements did not affect the abundance of corvid breeders (Estimate ± SE = -0.01 ± 0.06; CI 95 % = -0.14 — 0.12; -0.09 ± 0.08; -0.25 — 0.07, respectively), but affected the abundance of floaters (-0.32 ± 0.05; -0.42 — -0.23; -0.13 ± 0.06; -0.25 — -0.02, respectively). Considering the effect of the interaction between road density and hedgerow density (0.35 ± 0.05; 0.25 — 0.46), the abundance of corvid floaters decreased with hedgerow density when the road density was low and did not vary with hedgerow density when the road density was high (Appendix 7: Fig. S11). Considering the effect of the interaction between road density

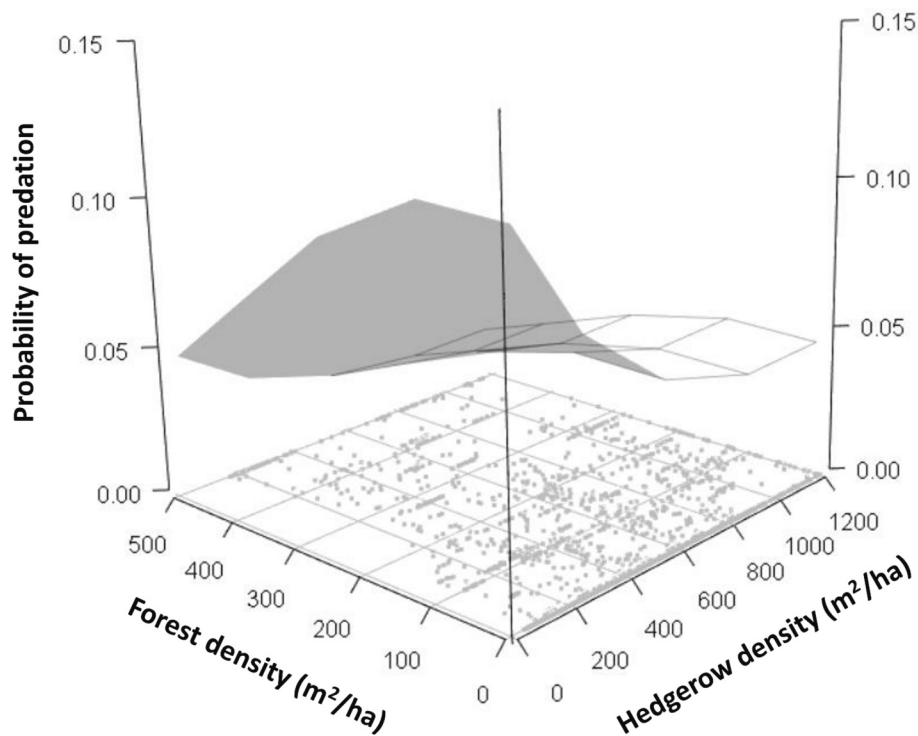


Fig. 3. Effects of hedgerow and forest densities on the probability of a nest being depredated by corvids. Predicted values (i.e., surface) are extracted from a GLMM detailed in Table 2. The grey and bottom points represent the distribution of observed values.

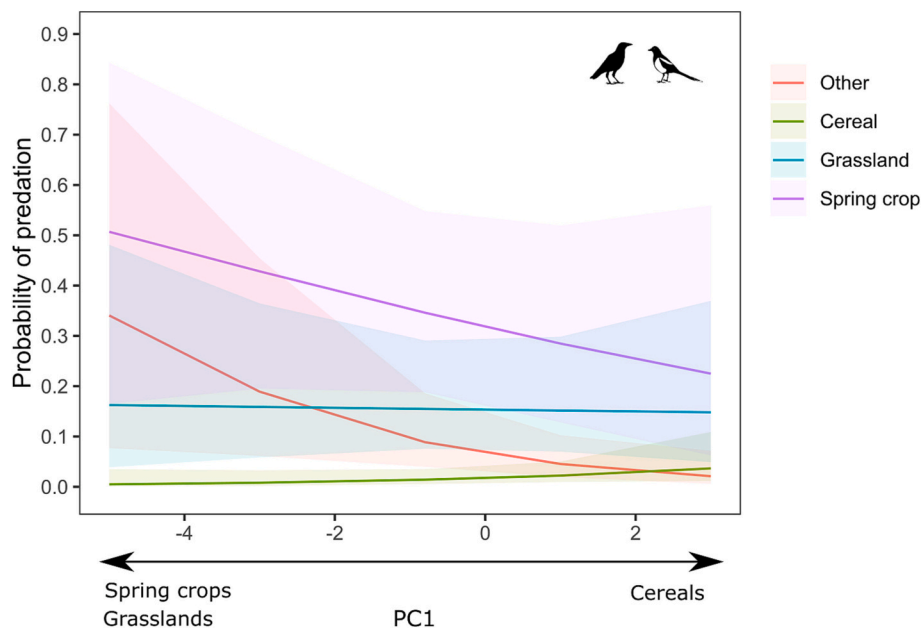


Fig. 4. Effect of land use as a gradient from grasslands and spring crops to cereals (indicated by the first axis of a principal component, PC1) on the probability of a nest being depredated by corvids splitting by the crop type in which nest was located (spring crop, grassland, cereal and other). Predicted values $\pm 95\%$ CI are extracted from a GLMM (Table 2). The first axis of the principal component analysis on land use proportions is detailed in Appendix 4.

and forest density (-0.19 ± 0.06 ; -0.31 — -0.07), the abundance of corvid floaters increased with forest density when the road density was low and did not change with forest density when the road density was high (Fig. S11). To conclude, many floaters were observed in areas with few roads and edges and many forest patches (Fig. S11).

3.3. Relationship between corvid abundance and predation rates

Corvid predation increased with corvid breeder abundance (Estimate \pm SE = 0.23 ± 0.05 ; CI 95 % = 0.13 — 0.32 , Appendix 8, Table S6), and did not with corvid floater abundance (0.00 ± 0.01 ; CI 95 % = -0.02 — 0.03 , Table S6). When corvid breeder abundance was included in the model of corvid predation, hedgerow density was no longer associated with corvid predation rate on eggs (-0.26 ± 0.14 ; CI 95 % = -0.55 —

Table 3

Effects of the distance to hedgerow, hedgerow density, forest density, their quadratic terms, land use from a principal component analysis (PCA), and two-way interactions on the abundance of corvid breeders (A) or floaters (B) using GLM (Poisson error distribution, link = logit). PC1 and PC2 are the first two axes of a principal component analysis on land use variables (see methods). PC1 describes a gradient from landscapes dominated by grasslands to the ones dominated by cereal crops (Appendix 4 Table S5) and PC2 from grasslands to spring crops (Appendix 4 Table S5).

Response variable	Explanatory variables	Estimate	SE	Lower CI	Upper CI
A. Corvid breeder	Hedgerow density	1.55	0.09	1.37	1.72
	Hedgerow density ²	-0.03	0.06	-0.15	0.09
	Forest density	0.14	0.06	0.02	0.26
	Forest density ²	0.29	0.13	0.04	0.54
	PC1	-0.42	0.12	-0.65	-0.19
	PC2	0.03	0.05	-0.07	0.13
	PC2	0.06	0.05	-0.05	0.16
	Hedgerow density × Forest density	-0.06	0.12	-0.30	0.17
	PC1 × Hedgerow density	0.05	0.05	-0.05	0.14
	PC1 × Forest density	-0.01	0.1	-0.20	0.18
	PC2 × Hedgerow density	0.08	0.04	0.00	0.16
	PC2 × Forest density	-0.13	0.1	-0.32	0.06
B. Corvid floater	Hedgerow density	1.71	0.07	1.56	1.85
	Hedgerow density ²	-0.41	0.05	-0.50	-0.32
	Forest density	0.23	0.05	0.14	0.32
	Forest density ²	-0.22	0.1	-0.42	-0.02
	PC1	0.33	0.09	0.15	0.50
	PC2	-0.24	0.04	-0.31	-0.16
	PC2	0.19	0.04	0.11	0.27
	Hedgerow density × Forest density	-0.1	0.08	-0.26	0.05
	PC1 × Hedgerow density	0.15	0.04	0.08	0.23
	PC1 × Forest density	-0.09	0.07	-0.22	0.05
	PC2 × Hedgerow density	0.02	0.03	-0.04	0.08
	PC2 × Forest density	0.33	0.07	0.19	0.47

0.02, Table S6). Consequently, corvid breeder abundance was associated with the effect of hedgerow density on corvid predation. Conversely, distance to hedgerow and PC1 remained associated with corvid predation since their odd ratios did not change much (Table S6). Finally, the model including corvid breeder abundance better explained the

variation of corvid predation (AIC = 1603.51) than the model with corvid floater abundance (AIC = 1623.34) or the model including only landscape variables without corvid abundance (AIC = 1621.34). Altogether, our results suggest that hedgerow density was a decisive driver shaping the abundance of corvid breeders in our study area and corvid predation rates of ground nests.

4. Discussion

At first sight, the use of artificial nests might appear to be limiting when examining the spatial variation of the predation rate, as they do not allow actual values to be extracted from wild conditions (Major and Kendal, 1996; Moore and Robinson, 2004). For instance, plasticine eggs may prevent predation due to their artificial scent, particularly in mammals. In our study area, corvids were the main nest predator, even when artificial nests were baited with natural eggs (Bravo et al., 2020). While we acknowledge the potential influence of odour associated with plasticine eggs, our results suggested that this effect might be negligible. Moreover, when standardised, the use of artificial nests has proven to be an efficient method for comparing predation patterns across different landscape attributes, hence assessing relative predation estimates rather than raw estimates. Artificial nests are a powerful and non-intrusive methodology allowing a large number of replicates.

Although the proximity of edges has largely been reported to shape the predation risk of forest birds (Andrén, 1995; Batáry and Báldi, 2004), the effect of landscape on the predation risk of ground-nesting species in open habitats remains unclear (Kaasiku et al., 2022; Lampila et al., 2005). Our study provides evidence that the farmland landscape configuration shapes both the abundance of mesopredators such as corvids and their predation rates on ground nests. Unlike corvid floaters, the abundance of corvid breeders (predicted mainly by hedgerow and forest densities), explained the variation of the ground nest predation rate by corvids. Indeed, variations in the abundance of corvid breeders and variations in nest predation rate by corvids were explained by similar landscape features, with the same slopes and signs. Therefore, our findings reveal that the predation rate by mesopredators in our study area is mainly driven by the effects of landscape structure, showing an effect of hedgerow and forest densities on the abundance of corvid breeders.

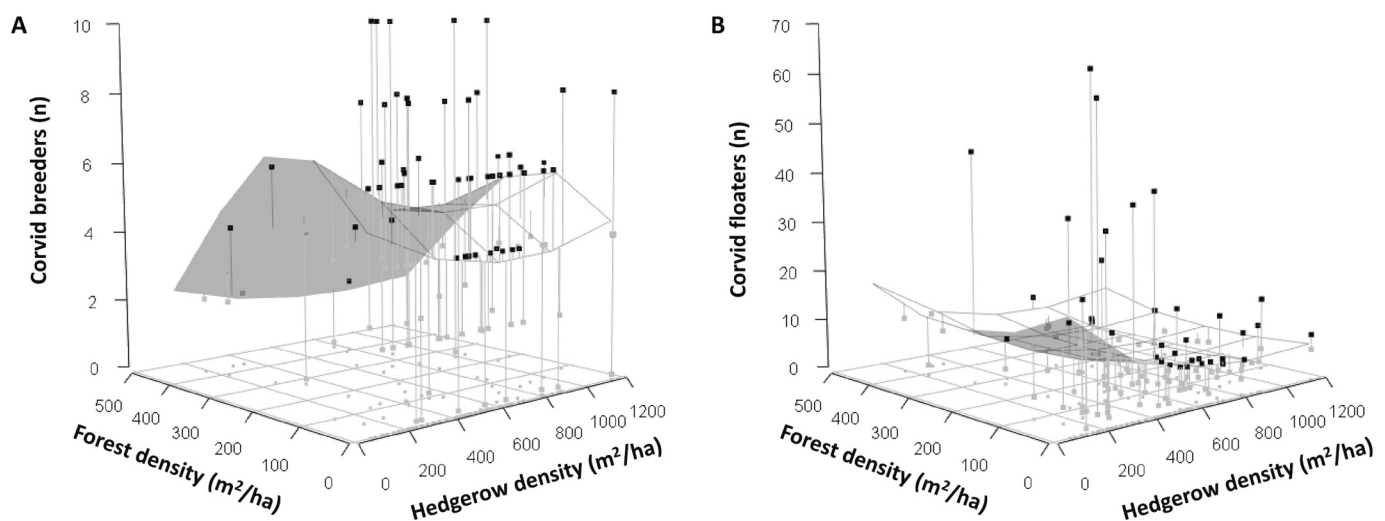


Fig. 5. Effects of the hedgerow and forest densities on the abundance of corvid breeders (A) and floaters (B). Predicted values (surface) are extracted from a GLM on breeders and floaters (detailed in Table 3A and B, respectively). Black and grey dots are the observed values that are respectively higher and lower than the predicted abundances of corvids. The bottom grey dots represent the distribution of observed values.

4.1. Effects of edge and forest

The predation rate was expected to increase when nests were close to hedgerows as mesopredators are known to increase their activity at habitat edges (Batáry and Báldi, 2004; Kaasiku et al., 2022). Our results supported this hypothesis, indicating that nest predators responded in different ways to edge proximity (Krüger et al., 2018; Lahti, 2001). Predation by other predators was consistently higher when closest to the hedgerow, regardless of the crop type, suggesting that hedgerows might play a role as corridors for predators such as mammals. However, in the case of corvid predation, the influence of edge proximity varied depending on the crop type in which the nests were located. Corvid predation was higher close to hedgerows when nests were in spring crops, whereas no significant effect of distance to hedgerows was observed for nests in cereal crops. This result suggests that the nest concealment provided by vegetation structure might be key for the nest predation by corvid in the proximity of hedgerows. Several studies failed to detect edge effects on nest predation in open landscapes (Donovan et al., 1997; Kaasiku et al., 2022) as it depends on landscape configuration, not only on the distance to edge per se (Batáry and Báldi, 2004; Chalfoun et al., 2002; Ludwig et al., 2012). Understanding the edge effect on predation patterns requires considering the landscape structure, including crop types, the availability of forest patches, and landscape connectivity (Chiavacci et al., 2018).

When hedges are lacking, landscapes with a density of forest around 100–200 m²/ha (i.e., only 2–3 % of the surface) had the highest probability of the nest being depredated by corvids. This pattern is supported by other studies that found higher densities of corvids (e.g., hooded crows *Corvus cornix*) in mixed landscapes (Smedshaug et al., 2002), suggesting that predators from forest patches spill over into cropped areas (Andrén, 1995). Predation rate by corvids decreased when the landscape became more forest-dominated (forest density of 500 m²/ha) which agreed with previous studies that showed high densities of corvids in agricultural-dominated landscapes (Andrén, 1992; Huhta et al., 1996). In contrast, the probability of a nest being depredated by other predators, such as mammals, was mainly influenced by the distance to hedgerows. Several studies reported that predation activity of mammals can concentrate on linear habitat features such as hedgerows, as they provide concealment and accessible travel routes through farmlands (Tryjanowski et al., 2002). Hence, while hedgerows and forest patches provide heterogeneity to the farmland landscape reducing predation pressure from corvids and providing benefits for the farmland biodiversity (Sirami et al., 2019), they may also enhance predation by other predators having detrimental effects on ground-nesting birds (Morris and Gilroy, 2008).

Although previous studies have reported that social status may affect the predation rate (Nilsen et al., 2009), few studies have examined the link between landscape, abundance of predators, social status, and predation rate. Our study found that the abundance of corvids with landscape configuration varied with their social status. While corvid breeders were set in territories that could be affected by landscape structure and food availability, floaters likely consisted of juvenile transient flocks that foraged over greater distances than breeders, which usually concentrate on foraging within smaller territories (Clayton and Emery, 2007). So, contrary to floaters, landscape structure shapes the spatial distribution of corvid breeders, and so does their predation rate on ground nests.

4.2. Effects of land use

Our results revealed that the predation rate of ground nests in farmland landscapes is influenced by the proportion of land use around the nest, suggesting a potential link between nest predation rates and the availability of alternative food for mesopredators (Laidlaw et al., 2013). For instance, agricultural intensification may lead to increased nest predation if it reduces the availability of alternative food such as insects

and seeds (Newton, 2004; Schmidt, 1999; Whittingham and Evans, 2004). Moreover, intensified agriculture may also result in a more uniform and dense vegetation structure (Wilson et al., 2005), which reduces nesting opportunities, but also predator accessibility. We found that the probability of a nest being depredated by corvids decreased when the landscape was dominated by cereal crops (i.e., uniform and dense vegetation with low alternative food), suggesting that corvids might actively avoid this kind of land use for searching for food (Saino, 1992). Cereal crops are poor food resource patches with low densities of worms, insects, and seeds (Díaz and Tellería, 1994) and their dense and tall vegetations makes them less accessible to corvids (Bravo et al., 2022), which mainly forage by walking on the ground and relying on visual cues. Nest predation by corvids and corvid abundance tended to decrease in landscapes dominated by grasslands. Although grasslands may provide more food resources than spring crops (Møller, 1983), they pose challenges for foraging due to dense vegetation, except when it is harvested. This result might reflect that corvids preferentially forage in spring crops, leading to higher predator activity and higher predation risk in these land uses. For ground-nesting birds, such as skylarks and lapwings, which preferentially nest in spring crops due to their sparse vegetation and bare soil (Berg et al., 2002; Chamberlain et al., 1999), this preference may create an ecological trap, increasing their vulnerability in a homogeneous landscape dominated by spring crops.

Our results showed that the probability of predation by other predators was not affected by the proportion of land use, suggesting that the effect of land use effect on the foraging strategies of generalist predators may vary depending on the predator species (Chiavacci et al., 2018). For example, in wet grassland landscapes, the rate of predation by foxes on wader nests might be reduced through the management of land uses by patches providing a high abundance of small mammals (Laidlaw et al., 2013). This is one of the few studies investigating the implications of land use and availability of alternative food resources on predation risk and suggests this is an area of conservation management that warrants critical attention.

The probability of corvid predation decreased throughout the breeding season in our study, suggesting that the increased vegetation growth likely made it more challenging for visually oriented predators, such as corvids, to locate nests. Conversely, our results suggested that other predators relying on olfactory cues, such as mammals, might not be affected by vegetation growth. The temporal variation in predation risk stresses the importance of considering dynamic processes when investigating nest predation rates as it may be important for the evolution of life history traits (e. g. the probability of laying replacement clutches may be affected by seasonal variation).

4.3. Effects of roads and buildings

Our findings indicate that the distance to human settlements did not have a significant impact on artificial nest predation rate. The presence of corvids and other predators, such as red foxes and stone martens, is likely to increase near human activities as they benefit from anthropogenic food resources (Bateman and Fleming, 2012; Manton et al., 2019; Marzluff and Neatherlin, 2006). Although their abundance may increase in urban environments, their predation rate may remain low, giving rise to an urban predation paradox (Fischer et al., 2012). Likely, the availability of easily accessible anthropogenic food resources might relax the predation rate close to human settlements (Rodewald et al., 2011), thereby contributing to the observed lower predation rates.

Our results revealed that road density tended to decrease the predation rate and the abundance of predators. Instead, we expected that road density increase corvid abundance and their nest predation as 1) road densities affect ground-nesting birds like grey partridges (Harmange et al., 2019) and little bustards (Cuscó et al., 2018) and 2) roads may be used by predators i) to move at night (Kautz et al., 2021) and ii) during daylight for opportunistic vertebrate species that actively search for carcasses from roadkills (Silva et al., 2019). Thus, the unexpected

relationship between road density, distance to human settlements, and the abundance of predators, as well as their predation rates, highlights the importance of considering anthropogenic features, when investigating the spatial dynamics of prey-predator interactions. The impact of roads and human settlements on predator-prey relationships is complex and warrants further investigation.

4.4. Perspectives for management

Although conservation actions toward ground-nesting birds tend to focus on control and exclusion of potential nest predators (Holt et al., 2008), much less attention has been paid to the management of landscape attributes that can potentially mitigate the impact of predators (but see Laidlaw et al. (2021)). The LTSER 'Zone Atelier Plaine & Val de Sèvre' is undergoing a major change in land cover. Cereal cover has increased by 20 % in the last 20 years against permanent components of the landscape (e.g., hedgerows) and grasslands (Bretagnolle et al., 2018). Our results showed that landscape homogenisation may favour the predation rate of generalist mesopredators such as corvids. A heterogeneous agricultural landscape that includes a mixture of crops associated with patches of forests, hedgerows and grasslands offering alternative food to generalist predators might reduce predation by corvids of ground-nesting birds. For instance, a forest density of 500 m²/ha reduced the likelihood of nest predation by corvids by 40 % and the corvid predation rate was also minimal with a hedgerow density of around 600 m²/ha or higher. Only 18 % and 8 % of our study area comprised forest density beyond 500 m²/ha and hedgerow density of 600 m²/ha, respectively. Thus, our study pleads for conservation actions of ground-nesting birds from landscape heterogeneity management.

Authors' contributions

Conceived and designed the experiments: CB VB OP MS. Performed the experiments: CB. Analysed the data: CB OP. Wrote the paper: CB OP MS VB.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank Alexandra Christin, Amandine Hamon, Mathias Noël, Manon Rescan, Emma Soulé, and Simon Trauet for their dedicated assistance during fieldwork. This project was supported by the Fédération Nationale des Chasseurs (FNC-PSN-PR20-2015). The CNRS provided additional funding. CB was also supported by a postdoctoral research contract for scientific excellence in the R&D Plan of the UCLM financed by the European Social Fund (ESF) and European Social Fund Plus (ESF+). We thank two anonymous reviewers for their constructive comments on a previous version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165712>.

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